

SIDEBAR 6.1. EVOLUTION OF FIRE ADAPTATIONS

Plant traits present in many fire-prone ecosystems have been interpreted as adaptations to fire. At the outset it is important to distinguish *adaptations* from *exaptations* (Gould and Vrba 1982). The former refers to traits that perform a particular function and have been selected for that function; the latter refers to traits that serve a particular function but that originated through selection for some other function. Distinguishing between the two is shaded by anthropogenic perspective—in many cases it is doubtful one can clearly distinguish between the two—and thus the term *apparent adaptation* may be appropriate.

The nature of fire adaptations is closely aligned with fire regime such that traits present in crown fire chaparral are far more similar to traits in other crown fire ecosystems such as boreal jack pine forests and South African fynbos than to adjacent ponderosa forests with a surface fire regime. In chaparral, crown sprouting and post-fire seed germination have been interpreted as fire adaptations. Sprouting in response to fire is almost certainly an exaptation as sprouting is nearly ubiquitous in dicotyledonous plants and likely has risen multiple times in response to many different processes (Keeley 1981). Relatively unique, however, are the large basal burls or lignotubers present in the chaparral species, *Adenostoma fasciculatum* and *Xylococcus bicolor*; and species of *Arctostaphylos*, *Ceanothus*, and *Garrya*. Although many woody species will produce ground-level tubers in response to various disturbances such as cutting, this coppicing effect is different because burls in chaparral species are normal ontogenetic structures that appear early in development.

Many chaparral species have fire-dependent reproduction with seed dormancy triggered by fire; this is likely a mix of adaptations and exaptations. Most species that recruit after fire can be classified as having heat-stimulated seeds or smoke- or charred wood-stimulated seeds (Keeley and Fotheringham 2000). High temperatures produced by solar heating of bare soil are sufficient to break dormancy in the former species, thus making this trait of selective value as a means of cueing germination to openings created by many types of disturbance. Smoke-stimulated germination would appear to be a clear adaptation to fire but the chemical cue in some species is nitrogen oxides that could be produced under other conditions. Another crown fire trait that is an apparent adaptation to fire is serotiny (Schwilk and Ackerly 2001), which is present in a few pines associated with chaparral, as well as lodgepole pine and jack pine, and widespread in mediterranean shrublands in South Africa and Western Australia (Lamont et al. 1991).

Surface fire regimes have selected for a very different suite of fire adaptations and generally these traits are not tied directly to reproduction. The dominant trees in most of our conifer forests and savanna woodlands have thick bark that is an apparent adaptation to fire. It has been argued that thick bark could have arisen in response to other environmental factors such as high and low ambient temperatures. However, the genus *Pinus* illustrates the overriding importance of fire in the determination of bark thickness. Also, all species from fire-prone habitats have very thick bark, whereas the desertic pinyon pines and the tree-line white pines have the thinnest bark (Keeley and Zedler 1998). The importance of fire regime characteristics is illustrated by the extraordinarily thick bark in savanna oaks compared with the rather thin bark in scrub oaks adapted to crown fire regimes (Zedler 1995). Typically in pines and oaks adapted to surface fire regimes, thick bark is also coupled with self-pruning of dead branches, traits that enhance survivorship of mature trees. This is critical since recruitment is often in post-fire environments and is dependent on the survival of parent seed trees.

One of the more controversial ideas related to fire adaptations is the hypothesis of species evolving characteristics that enhance flammability (Mutch 1970). Some have written this idea off as “group selectionist,” which is considered unlikely in the context of inclusive fitness theory that forms the basis of modern evolutionary theory. Bond and Midgely (2001) resurrected this idea and provided sufficient reasons to consider

it a possibility that flammability arose through effects on individual fitness. For example, in chaparral, some species such as chamise and species of manzanita and ceanothus fail to self-prune dead branches. It has been shown that this greatly affects fire intensity over what would occur if those branches were dropped and remained as surface fuels (Schwilk 2002). The selective advantage is that by contributing to higher-intensity fires, these species that are dependent on fire for reproduction may gain an advantage by creating greater openings for post-fire seedling recruitment.—*Jon E. Keeley*
